New perspective on the impact of aging on motor adaptation

Koenraad Vandevoorde, Jean-Jacques Orban de Xivry, *Dept. of Kinesiology, KU Leuven, Leuven, Belgium*

It is well established that the rate of motor adaptation declines with aging. This decline has been attributed to the degeneration of the cerebellum (Seidler *et al.*, 2006, 2007) or to instability of the motor memories (Trewartha *et al*., 2014). Yet, previous studies have always considered motor adaptation as a single process while we now know that it is composed of multiple processes such as implicit, explicit, error-based or model-free learning. Yet, insights into the impact of aging on these components of motor adaptation remain very limited. It is currently unknown which ones decline with aging and which ones are unaffected by it. In recent years, several paradigms have been developed to tear apart the different components of motor adaptation. Here, we use these established paradigms to study the influence of aging on the different components of motor adaptation. We present here the largest study ever conducted on the impact of aging on the different components of motor adaptation. More specifically, we investigated the sensitivity to errors using the paradigm developed by Marko *et al.* (2012) (Expe 1: 41 young and 40 elderly), the implicit and explicit components of motor adaptation using color cues as in Morehead *et al.* (2015) (Expe 2: 20 young and 20 elderly) and the stability of motor memories by looking at the retention of the motor memories as done by Hadjiosif & Smith (2013) (Expe 3: 21 young and 20 elderly).

Error-based learning can be assessed through single-trial learning and can be modelled by state-space equation (Eq.1). Single-trial learning is thought to measure the same process as the one governing overall motor adaptation. In experiment 1, we compared the direction of movements immediately before and after a trial with a visuomotor rotation (Fig.1A). The change in behavior reflects the sensitivity to the error experienced during the perturbed trial. This sensitivity is known to depend on the size of the experienced error. We reproduced the change in error sensitivity to error in young people (N = 41, age = 22.3 y ± 1.8, mean ± SD). Surprisingly, elderly people (N = 40, age 67.0 y ± 5.2, mean ± SD) were more sensitive to errors than their younger counterparts (Fig.1B, ANOVA, main effect of age, $p = 0.013$). That is, for a given error, the change in movement direction was larger for elderly than for young participants. All these participants were subsequently tested in motor adaptation experiments (Expe 2 - Nyoung = 20, Nold = 20 - or Expe 3 - Nyoung = 21, Nold = 20). These experiments consisted in a visuomotor rotation of 40° with continuous cursor feedback. In both these experiments (Fig.2B, Fig.3A), the rates of motor adaptation were lower for the elderly than for young people (t-test between lambda rates of exponential fitting to first learning block, Expe 2: $p = 0.002$; Expe 3: $p = 0.039$). In other words, elderly participants had higher sensitivity to errors but lower adaptation rates than younger ones.

In experiment 2, we measured the amount of explicit and implicit adaptation as done in Morehead *et al.* (2015). In this experiment, the participants voluntarily switched the explicit component of adaptation in function of the color of the cursor (Fig. 2A). The overall level of adaptation was clearly lower for elderly (Fig. 2B). In addition, the ratio implicit over explicit amount of learning was higher for elderly than for young people (Fig. 2C, ANOVA, main effect of age, $p = 0.004$). On the one hand, the amount of explicit learning was clearly decreased for elderly (Fig. 2C, ANOVA, Bonferroni-corrected post-hoc comparisons, $p < 0.001$). On the other hand, implicit learning seemed to be increased during the second learning block in elderly (Fig. 2C, ANOVA, Bonferroni-corrected post-hoc comparisons, $p < 0.001$). In addition, cue-evoked savings (first trial of relearning) were present both in young and elderly participants but was significantly smaller in elderly people than in the young ones (Fig. 2D, ANOVA, main effect of age, $p = 0.024$).

In experiment 3, we tested the stability of motor memory by interspersing one-minute breaks three times per learning block as done by Hadjiosif & Smith (2013) (Fig. 3B). These breaks allow us to separate the stable part of the motor memory (remaining motor memory after the break) from the overall part (learning level before the break). This stable component can be expressed as a percentage of the overall level of motor adaptation, the relative retention. This relative retention reflects the stability of the motor memory, which has been shown to be weaker in elderly people compared to younger ones (Trewartha *et al.*, 2014). However, the relative retention in motor adaptation due to the breaks was not significantly different between the two age groups (Fig. 3B, ANOVA, no main effect of age, $p = 0.38$).

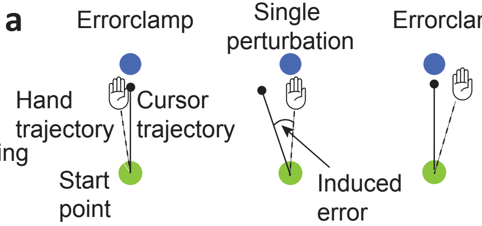
This set of studies brought a completely new perspective on the effect of aging on motor adaptation. First, we discovered that a deficit in error-based learning was not responsible for the lower adaptation rates observed in elderly. Rather, elderly participants significantly outperformed their younger counterparts at single-trial learning. Second, we confirmed that elderly participants do not re-aim as much as young participants but also found that their implicit component tended to be larger. Finally, we found that the stability of motor memories was not affected by age. Altogether, these studies debunked the idea that degeneration of the cerebellum is primarily responsible for the decline in motor adaptation observed in elderly people. In contrast, the decline in motor adaptation is mostly due to a deficit in the re-aiming strategy, and, surprisingly, might be partially compensated by error-based learning and implicit adaptation.

References. 1. 2. Seidler, *et al.* (2006, 2007). 3. Trewartha, *et al.* (2014). 4. Marko, *et al.* (2012). 5. Morehead, *et al.* (2015). 6. Hadjiosif & Smith (2013, TCMC)

Equation 1. State-space equation.

$$\hat{x}^{(n+1)} = a\hat{x}^{(n)} + \underbrace{\boxed{\eta(e)^{(n)} e^{(n)}}}_{\text{Error-based learning}}$$

$\hat{x}$: Estimate of perturbation
a: Retention factor
e: Sensory-prediction error
η: Error sensitivity parameter
x: Perturbation



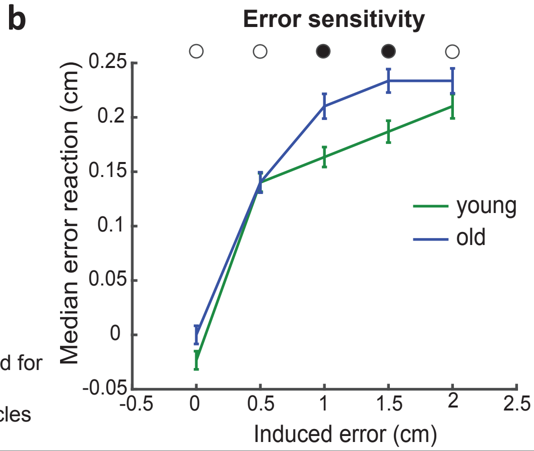
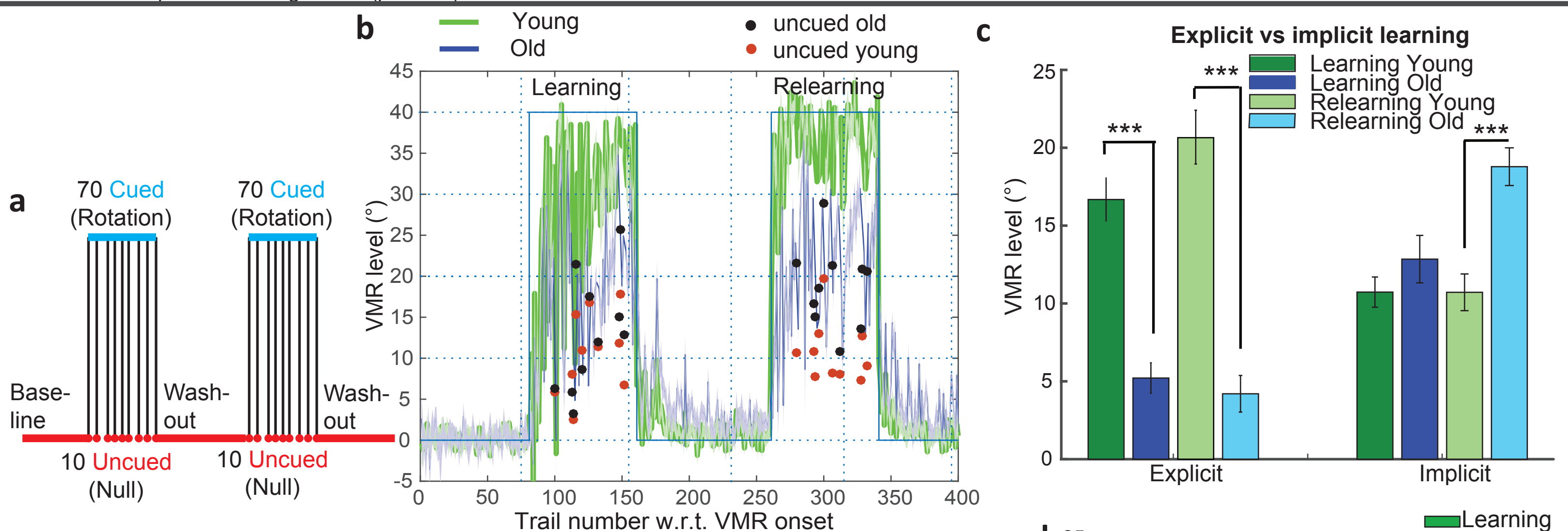


Figure 1: Older participants learn more from errors than younger participants in a single-trial learning paradigm. Equation 1: Error-based learning can be modelled by state-space equation. The error sensitivity parameter, η(e), in this equation explains how much a subject learns from a specific error.
a: Single-trial error-based learning can be assessed to determine the error sensitivity parameter for young and elderly. Triplets of a visual errorclamp, a single-trial perturbation and another visual error-clamp were used to determine the reaction to error for single specific error sizes. **b:** Unexpectedly, sensitivity to errors was increased for older (n = 40) compared to young subjects (n = 41) for certain induced error sizes (ANOVA, main effect of age, p = 0.013). Black circles indicate the post-hoc comparison between young and old for each error size. Filled circles indicate that comparison was significant (p < 0.05).



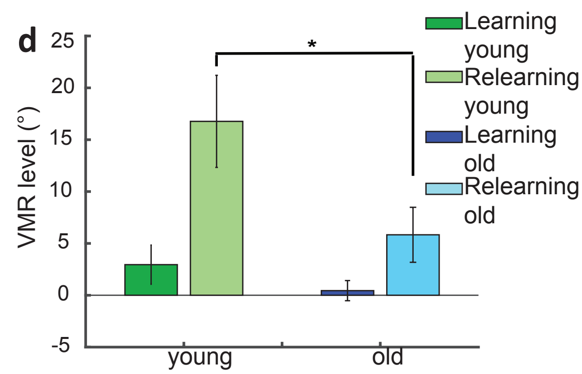


Figure 2: Explicit learning is decreased in elderly, while implicit learning is increased. a: Perturbation schedule for distinguishing explicit and implicit learning with cursor cues.
b: Overall adaptation of young (n = 20) and old (n = 20) participants. During the uncued trials in the two learning blocks the participants voluntarily removed their explicit part of adaptation. Therefore, the remaining adaptation level was the implicit part of adaptation. **c:** Explicit versus implicit learning for young and elderly. Explicit learning was decreased for elderly in both learning blocks, while implicit learning was increased for elderly in the second learning block. The amount of implicit learning was calculated as the average of the 10 uncued (no-perturbation) trials. The amount of explicit learning was calculated by subtracting the implicit learning from the overall learning. For the overall learning the 10 cued (perturbation) trials preceding the 10 uncued trials were used. This procedure was performed for each learning block for young and old and showed significant age effects (ANOVA, main effect of age, p < 0.001, and post-hoc comparisons, p < 0.001 (***)). Error bars are SEM. **d:** A significant amount of cue-evoked savings is present from the first trial of relearning in both young and old subjects. However, the amount of cue-evoked savings was significantly smaller in old compared to young subjects (p = 0.024 (*)).

Figure 3: Relative retention of motor memory is not different for young and elderly. a: Similar setup as in Hadjiosif & Smith (2013) for studying stability of motor memory. Every 30-40 trials a 1 minute break was applied. After this 1 minute break the stable visuomotor rotation (VMR) level was obtained. The stable VMR level after the break could be compared to the overall VMR level before the break to determine the relative retention (%) of motor memory for young (n = 21) and elderly (n = 20). **b:** Relative retention (%) of motor memory was not different between young and old subjects (ANOVA, main effect of age, p = 0.38). The relative retention was calculated for each of the three pauses in the two learning blocks.